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Endophyte grasses

As an endophyte, a fungus may grow within a plant in a mutualistic relationship. Two notable examples are tall fescue (*Festuca arundinacea*) infected with the fungus *Neotyphodium coenophialum* (formerly *Acremonium coenophialum* and *Epichloe typhina*) and perennial ryegrass (*Lolium perenne*) infected with the fungus *Neotyphodium lolii*. This mutualistic relationship benefits the fungus through provision of energy, nutrients, shelter, and a means of propagation, while it benefits the plant with mechanisms for improving persistence through biochemical deterrents to overgrazing and insect damage.

Identification of the fungus. Tall fescue was widely planted in the United States during the 1940s and 1950s following the release of the variety Kentucky-31 in 1943 by E. N. Fergus of the University of Kentucky. This grass filled a void in the southern states, where few other cool-season forages were adapted. However, cattle grazing tall fescue often developed a chronic health condition, which was especially apparent in the summer (called summer syndrome or summer slump). Beginning in 1973, a farm near Mansfield, Georgia, provided the background for J. D. Robbins and C. W. Bacon to discover the reason why one cattle herd on the farm exhibited summer syndrome while another herd did not. Animals suffering from fescue toxicosis were consuming tall fescue with all plants infected with the endophytic fungus, while unaffected animals were consuming tall fescue in a pasture with only 10% of the plants infected with the endophyte.

Spread of the fungus. The endophytic fungus spreads to other plants only through seed dispersion of infected plants and is not known to be culturable outside the host plant. A common method of removing the fungus from host plants is to store seeds at room temperature for a year following harvest, so that the fungus dies, and then to plant the remaining viable seeds. The fungus does not change the growth or appearance of the host grass, and therefore detection of the fungus requires laboratory analysis, often by staining and observation of leaf sheath tissue under a microscope (**Fig. 1**).

Tall fescue is grown on about 14 million hectares (35 million acres) of land in the United States and at least the same area in other parts of the world, including Europe, Asia, and northern Africa. Surveys in the United States indicate a high frequency of endophyte infection on most tall fescue pastures. Seeds from a number of varieties of tall fescue are currently being



Fig. 1. Stained serpentine *Neotyphodium coenophialum* mycelia occupying the spaces between cells of a tall fescue leaf sheath. Magnification 400 \times . (Courtesy of Nicholas Hill)

sold with low infection frequency of the endophyte for those producers that want to avoid the negative impacts of endophyte infection.

Animal response. Farm animals grazing endophyte-infected tall fescue can suffer from a number of health disorders, including fescue foot, fat necrosis, and fescue toxicosis. Documented animal responses to consumption of endophyte-infected tall fescue include (1) lower feed intake, (2) lower weight gain, (3) lower milk production, (4) higher respiration rate, (5) higher core body temperature, (6) rough hair coat, (7) more time spent in ponds or puddles, (8) more time spent in shade, (9) less time spent grazing, (10) excessive salivation, (11) reduced blood serum prolactin level, and (12) reduced reproductive performance. Reduced animal performance and productivity are linked to toxic ergopeptine alkaloids that accumulate in endophyte-infected leaf tissue. Symptoms of toxicity are most prevalent during the hot summer months and less prevalent during the cool autumn and spring months.

Ecological benefits of association. Both tall fescue and perennial ryegrass are cool-season grasses, which begin to grow during the cool autumn months, survive the winter in a green state depending upon the severity of cold, resume growth in early spring, and flower in late spring prior to the heat of summer. The long hot summers in the southeastern United States limit the ability of most cool-season grasses to persist for more than a few years. Tall fescue, however, persists with cattle grazing in the southeastern United States better than most other cool-season forages, probably because of association with the endophyte. Research suggests that endophyte-infected tall fescue is more productive and able to survive drought better than uninfected tall fescue.

There have been a number of documented cases of resistance to pest infestation and damage in endophyte-infected perennial ryegrass and tall fescue stands compared with endophyte-free stands. These cases include responses to Argentine stem weevil, black beetle, sod webworm, aphids, fall armyworm, pasture mealybug, cutworm, and spiral nematodes.

The effect of the endophyte may go far beyond that solely in the immediate vicinity of the plant. Recent research from long-term tall fescue pastures in Georgia indicates that endophyte-infected pastures could be putting more of the carbon captured by photosynthesis of the plant into the soil as organic matter, rather than respiring the carbon back into the atmosphere as carbon dioxide.

Carbon dioxide is fixed by plants during photosynthesis into simple sugars, which are then metabolized into higher-level organic compounds needed by the plant. Plants respire part of the carbon back into the atmosphere as carbon dioxide to generate metabolic energy, and the remainder leads to growth of the plant. Following death, plant tissues are attacked by soil bacteria, fungi, and various other organisms that use this organic material as energy and carbon sources for their own growth. These organ-

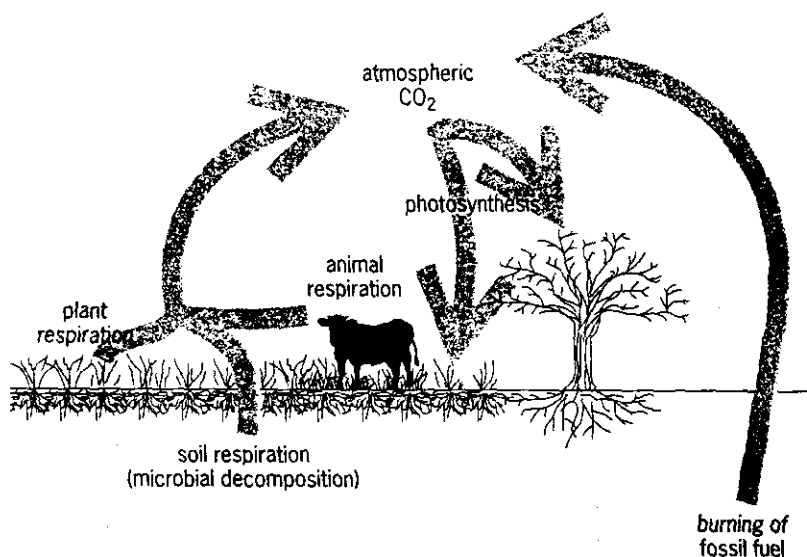


Fig. 2. Simplified diagram of the carbon cycle. Carbon dioxide is fixed by plants through photosynthesis and returns to the atmosphere when organisms (plants, animals, and microbes) respire.

isms decompose organic material, returning a portion of the organically bound carbon to the atmosphere as carbon dioxide (microbial respiration) and transforming the remainder into microbial biomass and more inert forms of soil organic matter or humus. Photosynthesis and respiration are major components of the global carbon cycle that have kept the level of carbon dioxide in the atmosphere at a relatively constant level (Fig. 2). Rising atmospheric carbon dioxide levels during the past century indicate an imbalance in the carbon cycle that could lead to global warming and widespread ecological changes. Sequestration of carbon in the soil as organic matter is a management strategy that could be employed by individual land owners on a large enough scale to help mitigate this rise in atmospheric carbon dioxide.

In pastures near Watkinsville, Georgia, cattle had been grazing Kentucky-31 tall fescue with low and high endophyte infection in one set of replicated paddocks for 8 years and another set of paddocks for 15 years. During these periods, total organic carbon had accumulated near the soil surface under both low- and high-endophyte-infected tall fescue, but more so with high endophyte infection (Fig. 3). Greater total soil organic carbon under high endophyte infection was also associated with greater total nitrogen in soil and lower soil bulk density, but lower potential soil microbial activity (see table). Commonly however, potential soil microbial activity changes proportionally with changes in total soil organic carbon. The observation that total soil organic carbon was greater with high endophyte infection, but potential soil microbial activity was lower than with low endophyte infection, suggests that various ecological changes occurred in the soil in response to the presence of the endophyte. Possible responses

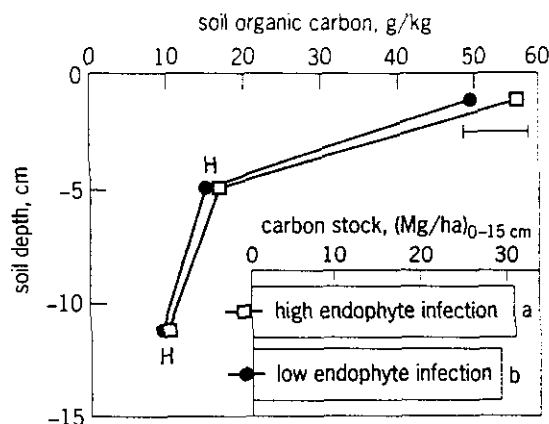


Fig. 3. Concentration of soil organic carbon with depth under low and high endophyte infection of tall fescue and carbon stock at a depth of 0–15 cm. Error bars within a soil depth indicate significance at probability (p) ≤ 0.05 . Letters a and b beside bars in inset indicate significant difference at $p = 0.01$. (Data from A. J. Franzluebbers et al., *Soil carbon and nitrogen pools under low- and high-endophyte-infected tall fescue*, *Soil Sci. Soc. Amer. J.*, 63:1687–1694, 1999)

include (1) direct inhibition of the ability of soil microorganisms to decompose the additional alkaloid compounds present in endophyte-infected tall fescue residues; (2) direct selection of specific microbial groups that could have formed specific intermediate degradation products, which may have resisted further breakdown; (3) indirect changes in the community of soil microorganisms, of which the multitude of bacteria, fungi, and protozoa have different abilities to coexist and process soil organic matter; and (4) indirect changes in the quantity, quality, and timing of carbon translocated to roots and root exudates, which provide a portion of the carbon source for soil microbial and faunal activity. All of these possible responses could have led to accumulation of total soil organic carbon and nitrogen in soil with endophyte infection.

One response of animals to the consumption of endophyte-infected tall fescue is to spend more time in the shade and less time foraging. This behavior can lead to an accumulation of nutrients (such as phosphorus and magnesium) in soil near the shade and water sources of pastures. Redistribution of nutrients within pastures is common as animals consume forage throughout the pasture, but spend more time drinking, lounging, and defecating near shade and water sources. Concentration of nutrients near shade and water sources in endophyte-infected pastures is, therefore, exacerbated due to animal behavior.

Endophyte-enhanced varieties of grasses have recently become of great interest to researchers trying to retain the beneficial aspects of the association while removing the negative aspects. Plant-fungi genetic combinations are being sought that keep the biochemical codes necessary for maintaining plant persistence but reduce or delete the biochemical compounds responsible for causing animal health disorders. A great deal has been learned about plant and animal responses to endophytes during the past 30 years; however, short- and long-term ecological impacts of endophytes are only beginning to be discovered.

For background information see ALKALOID; BIO-DEGRADATION; FESCUE; FUNGI; GRASS CROPS; SOIL CHEMISTRY in the McGraw-Hill Encyclopedia of Science & Technology.

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Soil properties (0–15-cm depth) under tall fescue as affected by endophyte infection level*

Soil property	Endophyte level		
	Low	High	Significance†
Soil bulk density, $\text{Mg} \cdot \text{m}^{-3}$ soil	1.27	1.25	0.02
Total organic carbon (TOC), $\text{g} \cdot \text{kg}^{-1}$ soil	15.3	16.8	<0.01
Total nitrogen, $\text{g} \cdot \text{kg}^{-1}$ soil	1.12	1.23	<0.01
Potential microbial activity, $\text{mg CO}_2\text{-C} \cdot \text{kg}^{-1}$ soil	28.1	25.7	0.16
Specific microbial activity, $\text{g CO}_2\text{-C} \cdot \text{kg}^{-1}$ TOC	1.87	1.57	0.01

*Data from A. J. Franzluebbers et al., Soil carbon and nitrogen pools under low- and high-endophyte-infected tall fescue, *Soil Sci. Soc. Amer. J.*, 63:1687–1694, 1999.

†Significance is probability that the magnitude of difference between means would occur again if values were random.